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NEPHROPS NORVEGICUS: COMPARATIVE BIOLOGY AND FISHERY IN THE MEDITERRANEAN SEA. *F. SARDÀ (ed.)*

Genetic structure of Norway lobster, *Nephrops norvegicus* (L.) (Crustacea: Nephropidae), from the Mediterranean Sea*

FERRUCCIO MALTAGLIATI, LAURA CAMILLI, FRANCO BIAGI and MARCO ABBIATI

Università di Pisa, Dipartimento di Scienze dell'Uomo e dell'Ambiente, Via A. Volta 6, I-56126, Pisa, Italy.

SUMMARY: The population genetic structure of the Mediterranean Norway lobster was studied by means of cellulose acetate allozyme electrophoresis. Populations from one Atlantic and eight Mediterranean localities were sampled. The 15 enzyme systems analysed gave 23 presumptive gene loci, 11 of which were polymorphic. The analysis of genotypic and allelic frequencies revealed levels of genetic polymorphism comparable with those of studied decapods: mean heterozygosities ranged from 0.052 (*se* 0.025) to 0.142 (*se* 0.040). The values of Nei's genetic distance index showed moderate genetic differentiation between geographical regions and no geographical pattern of genetic differentiation was detected by UPGMA cluster analysis. Moreover no clear clines in allelic frequencies were detected, thus genetic variability seems to be randomly distributed among populations and *Nephrops norvegicus* seems to follow the island model of genetic structure. The degree of genetic subdivision of the species is confirmed by the mean value of the standardised variance in allelic frequencies (F_{ST} = 0.122), giving an estimate of gene flow, Nm = 1.80.

Key words: Allozyme electrophoresis, genetic variation, genetic distance, population subdivision, island model, *Nephrops norvegicus,* crustaceans, Mediterranean.

RESUMEN: ESTRUCTURA GENÉTICA DE LA CIGALA *NEPHROPS NORVEGICUS* (L., 1758) (CRUSTACEA: NEPHROPIDAE), EN EL MEDITERRÁNEO. – La estructura genética poblacional de la cigala (*Nephrops norvegicus*) se estudió mediante electroforesis alocímica en acetato de celulosa. Las muestras analizadas provienen de ocho localidades del Mediterráneo y una del Atlántico adyacente. En un total de 15 sistemas enzimáticos se detectaron 23 loci, de los cuales 11 resultaron polimórficos. La heterozigosis media detectada varía desde 0,052 (*se* 0,025) a 0,142 (*se* 0,040) y es similar a la observada para otros decápodos. Las distancias de Nei muestran una moderada diferenciación genética, sin embargo el análisis de agrupamiento UPGMA no revela ningún patrón geográfico. No se detectaron clinas en las frecuencias alélicas, la variabilidad genética parece presentar una distribución al azar y la estructura genética de la cigala parece seguir el modelo de insularidad. El valor promedio de F_{ST} = 0,122 confirma un cierto grado de subdivisión genética e indica un flujo génico estimado de Nm = 1,80.

Palabras clave: Electroforesis, variación genética, distancia genética, subdivision de población, *Nephrops norvegicus,* crustáceos, Mediterráneo.

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INTRODUCTION

The study of the genetic structure is important for species of ecological and commercial importance. Genetic substructuring of a species indicates population heterogeneity; conversely, genetically homogeneous populations over large geographic regions have no significant population structuring. In the marine environment, gene flow typically occurs through the movement of gametes, larvae, or adults. In absence of selection, microevolutionary forces, such as gene flow and genetic drift, determine the genetic homogeneity or heterogeneity of the species (Slatkin, 1985). The genetic substructuring of the species is an important component for the management of harvested species and might be used to predict whether a locally depleted population will be successfully repopulated by immigrants (Utter, 1991). For example, the genetic consequences of the loss of one portion of a species are quite different if the species has a panmictic population structure as opposed to a highly subdivided one.

The Norway lobster, *Nephrops norvegicus* (L., 1758), is a species of high commercial interest in the Mediterranean. It is a marine benthic crustacean with a wide geographical distribution. It occurs in the North Sea, reaching northern Norway, in the NE/E Atlantic Ocean from Greenland to Morocco and in the whole Mediterranean. The bathimetric distribution of the species varies among different geographic areas ranging from 15 to more than 500 meters in depth. At present growing attention exists for this species, both as an exploitable resource and for conservation purposes. Differences in morphological traits (mean individual size, growth rate) and in reproductive characteristics (size at first sexual maturity, latitudinal variation in the ovarian cycle, period of egg incubation and in periodicity of female spawning, fecundity within and among populations) have been documented (Gamulin-Brida *et al*., 1972; Froglia and Gramitto, 1981, 1987; Sardà, 1995). These differences might be due to phenotypic responses both to different environmental conditions and to intensive fishing pressure, or to genetic differences. Corni *et al*. (1989) observed differences in the number of chromosomes in specimens collected at two localities in the Adriatic Sea; this genetic characteristic was explained by Deiana *et al*. (1996) by the presence of supernumerary chromosomes in this species. However, population differentiation was not supported by a preliminary population genetic study, based on small sample size, for allozyme characterisation of two Adriatic samples of Norway lobster (Mantovani and Scali, 1992). Moreover, recent genetic studies on Mediterranean populations of the pink shrimp, *Aristeus antennatus*, another decapod showing variability in morphometric traits, detected extensive genetic homogeneity (Sardà *et al*., 1998).

Despite the remarkable commercial value of *N. norvegicus*, some characteristics of its life cycle, as for example the larval behaviour and the dispersal capability, are scantily known for Mediterranean populations. Research on larval behaviour conducted in the Irish Sea showed that the life-span of planktonic larvae is about fifty days (Hill, 1990). The dispersal capabilities of larvae are strictly dependent on sea currents: in the Irish Sea larvae are retained in surface waters over adult grounds by a whirlpool effect present in that region, preventing a massive dispersal to other sites (Hill *et al*., 1994). However, in regions different from the Irish Sea, pelagic dispersal may lead to opportunities for colonisation of distant mud patches (Hill, 1990).

If there are self-sustaining stocks in the different geographical regions where the Norway lobster is found, a severe exploitation may lead to the extinction of local populations. The consequences may be less severe if a major portion of individuals in one area is provided by planktonic larvae spawned elsewhere. In order to elucidate the general pattern of the population structuring of Norway lobster, a program was carried out with the aim of studying the genetic variation among populations in areas of intensive commercial fishing, such as European regions of the Mediterranean and an Atlantic one, off South Portugal. Thus, we would verify by biochemical markers (allozymes) whether *N. norvegicus* has a wide genetic uniformity, or if it is possible to identify separate genetic stocks.

MATERIALS AND METHODS

Sampling

Sampling was designed to determine the genetic structure and the degree of genetic differentiation of Norway lobster in the Mediterranean. Specimens were caught by bottom trawl nets in one Atlantic and eight Mediterranean localities (Fig. 1; Table 1). Each sample consisted of roughly 100 individuals, all coming from only one haul. Specimens were put in individually numbered plastic bags, transferred to the laboratory in dry ice and stored at -80°C until analyses.

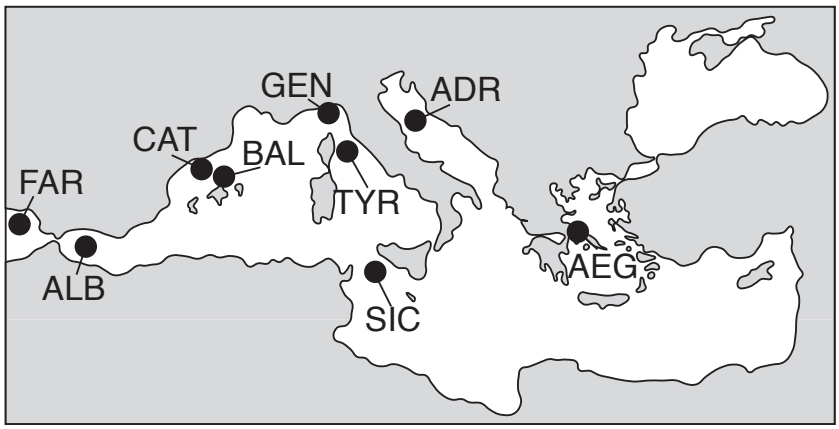

FIG. 1. – Location of sampling sites. Abbreviations for localities are as in Table 1.

TABLE 1. – Principal characteristics of the sampling trawls. *La* and *Lo* are the latitude and the longitude of the beginning of the trawls respectively; *D* is the average depth of the trawls.

Locality	*Abbrev.*	*Date*	*La*	*Lo*	*D*
Adriatic Sea	ADR	24/01/1994	43°54'N	13°50'E	70 m
Aegean Sea	AEG	11/01/1994	38°40'N	23°26'E	120 m
Alboran Sea	ALB	10/01/1994	35°30'N	04°20'W	400 m
Balearic Islands	BAL	15/03/1994	39°37'N	02°02'E	430 m
Catalan Sea	CAT	09/01/1994	41°06'N	02°11'E	500 m
Faro (Atlantic)	FAR	10/01/1994	36°47'N	07°57'W	400 m
Ligurian Sea	GEN	08/03/1994	44°04'N	09°26'E	520 m
Sicily Channel	SIC	10/02/1994	36°30'N	13°30' E	400 m
Tyrrhenian Sea	TYR	10/02/1994	42°26'N	10°44'E	270 m

Electrophoresis

Samples of chela muscle and hepatopancreas tissue were dissected after thawing. Extracts were prepared by mincing tissues in an equal amount of a pH 8.0 extracting buffer (0.2 M Tris, 1 mM EDTA and 25 mM 2-mercaptoethanol) by means of a rotating potter pestle. Homogenates were centrifuged at 4000x*g* for 10 minutes, then the supernatant was separated for electrophoresis. Care was taken to keep sample temperature below 5°C at all stages of preparation. Cellulose acetate electrophoresis was used to survey the enzyme systems listed in Table 2. Electrophoresis was performed at 300 volts for 25 minutes, using a Tris-EDTA-Maleate (TEM) buffer system (Schneppenheim and Mac Donald, 1984) for all enzymes. Preliminary analyses were carried on three tissues (abdomen muscle, chela muscle and hepatopancreas). Abdomen and chela muscle gave comparable resolution, thus chela muscle was chosen for its practicality. For LDH and PGM, hepatopancreas gave two additional loci unexpressed in the muscle, thus these two enzyme systems were analysed for both tissues. Enzyme staining was carried out according to slightly modified procedures described by Pasteur *et al.* (1988). When an enzyme is encoded by two loci in one tissue, the more anodally migrating isoenzyme is suffixed as 1. For each locus the most common allele was designed as 100; additional alleles were assigned numerical values according to their distance from the allele 100. An initial electrophoretic screening was carried out using thirty specimens each population, in order to detect polymorphic loci; loci showing only one allele in this subsample of individuals were not analysed in the remaining specimens and were considered as monomorphic.

TABLE 2. – Enzyme systems used for allozyme electrophoresis. EC number according to IUBNC (1984).

Abbrev.	Enzyme system	EC No.
ALD	aldolase	4.1.2.13
AO	aldehyde oxidase	1.2.3.1
GAPDH	glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12
αGPD	α-glycerophosphate dehydrogenase	1.1.1.8
G6PDH	glucose-6-phosphate dehydrogenase	1.1.1.49
GPI	glucose-6-phosphate isomerase	5.3.1.9
IDH	isocitrate dehydrogenase	1.1.1.42
LDH	L-lactate dehydrogenase	1.1.1.27
MDH	malate dehydrogenase	1.1.1.37
ME	malic enzyme ($NADP^+$)	1.1.1.40
MPI	mannose-6-phosphate isomerase	5.3.1.8
PGD	phosphogluconate dehydrogenase	1.1.1.44
PGM	phosphoglucomutase	5.4.2.2
SDH	sorbitol dehydrogenase	1.1.1.14
XDH	xanthine dehydrogenase	1.2.1.37

Statistical analyses

Genotypic data were analysed using the computer package BIOSYS-1 (Swofford and Selander, 1981). Allele frequencies, mean number of alleles per locus, percentage of polymorphic loci (0.99 criterion), and mean heterozygosity (direct count and expected from Hardy-Weinberg equilibrium) were calculated for each sample. Genotype frequencies of each sample were tested at all polymorphic loci for deviation from Hardy-Weinberg equilibrium values using a chi-square goodness of fit test on observed genotype frequencies. Levels of genetic differentiation between populations were estimated by Nei's (1978) genetic distance. This index takes a range from 0 (total similarity) to infinity (total dissimilarity), and its unbiased estimates take sample size into account.

Wright's (1978) *F*-statistics was used to estimate the levels of population structuring. The basic formula of *F*-statistics is $1\text{-}F_{IT} = (1\text{-}F_{IS})(1\text{-}F_{ST})$. F_{IT} is the correlation coefficient between uniting gametes relative to the whole array of samples; F_{IS} is the correlation coefficient between uniting gametes within populations; F_{ST} (the standardised genetic variance in allele frequencies) is the correlation of two randomly chosen alleles in a population relative to alleles in the whole array of samples.

The values of F_{IS} and F_{IT} are negative when there is an excess of heterozygotes and positive for a deficiency of heterozygotes in single populations and in the whole array of samples, respectively. Significance of F_{ST}, F_{IT}, and F_{IS} was tested according to the following methods:

$$\chi^2 = F_{IS}^2 N(k\text{-}1),\ \text{d.f.} = \frac{k(k\text{-}1)}{2}\ \text{(Li and Horvitz, 1953)}$$

$$X = \left|F_{IT}\right| \sqrt{N} \quad \begin{matrix} X > 1.96,\ P < 0.05 \\ X > 2.57,\ P < 0.01 \end{matrix}\ \text{(Brown, 1970)}$$

$\chi^2 = 2\ N\ F_{ST}\ (k\text{-}1)$, d.f. = $(k\text{-}1)(s\text{-}1)$ (Workman and Niswander, 1970)

where *N* is the total number of individuals sampled, *k* is the number of alleles and *s* is the number of localities analysed for each locus.

We used the standardised genetic variance F_{ST} to calculate an estimate of gene flow (*Nm*, the effective number of migrants per generation) according to Wright's (1943) island model formula: $F_{ST} = 1/(4Nm+1)$.

RESULTS

Fifteen enzyme systems gave twenty-three clearly recognisable presumptive gene loci. Eleven loci (*Sdh-2, Sdh-3, Ldh-1, Ldh-2, Me, G6pdh, Xdh-1, Xdh-2, Ao, Pgm-1, Pgm-2*) were polymorphic (frequency of most common allele ≤ 0.99) in at least one sample. Allelic frequencies are shown in Table 3. No private alleles were detected. Only *Sdh-3* and *Me* were closely fixed for the same allele in all populations sampled. All the other systems showed two allelic variants, one of which was relatively rare at loci *Ldh-1* and *G6pdh*. The loci *Ldh-2*, *Ao*, *Pgm-1* and *Pgm-2* presented one allele much more frequent than the other in all populations, while for *Sdh-2*, *Xdh-1* and *Xdh-2* the two variants were at intermediate frequencies in several populations. At some polymorphic loci, the most common allele was fixed in a few populations. For example, $Sdh\text{-}2^{100}$ was fixed in the Faro and Genoa samples, $Ldh\text{-}2^{100}$ was fixed in the Catalan Sea sample, $G6pdh^{100}$ was fixed in the Faro sample and Ao^{100} was fixed in the Faro and Sicily Channel samples.

Mean heterozygosities for Mediterranean populations ranged from 0.063 ± 0.030 to 0.142 ± 0.040, the Atlantic population from Faro displaying the lowest mean heterozygosity (0.052 ± 0.025) (Table 4). The lower genetic variability for Faro population, as measured by mean heterozygosity, was also confirmed by the lowest mean number of alleles per locus (1.3 ± 0.1) and the lowest percentage of polymorphic loci (30.1%), which ranged from 1.3 ± 0.1 to 1.5 ± 0.1 and 34.8% to 43.5%, respectively (Table 4) in the Mediterranean populations.

TABLE 3. – Allele frequencies at eleven polymorphic loci[a] for nine populations of *Nephrops norvegicus*. *n* is number of individuals analysed per locus; mc is the muscle of chela and hp is the hepatopancreas; *A* is the allele number. Population abbreviations are as in Table 1.

Locus	Tissue	*A*	ADR	AEG	ALB	BAL	CAT	FAR	GEN	SIC	TYR
Ao	mc										
n			69	94	73	88	87	50	83	83	100
		100	0.616	0.947	0.767	0.920	0.937	1.000	0.958	1.000	0.990
		98	0.384	0.053	0.233	0.080	0.063	-	0.042	-	0.010
G6pdh	hp										
n			89	95	73	95	98	59	90	67	77
		100	0.927	0.932	0.890	0.937	0.934	1.000	0.972	0.978	0.922
		98	0.073	0.068	0.110	0.063	0.066	-	0.028	0.022	0.078
Ldh-1	mc										
n			83	84	82	80	77	83	90	71	70
		100	0.940	0.976	0.945	0.950	0.981	0.952	0.967	0.986	0.964
		98	0.060	0.024	0.055	0.050	0.019	0.048	0.033	0.014	0.036
Ldh-2	hp										
n			69	89	98	67	104	88	77	58	65
		100	0.768	0.876	0.995	0.754	1.000	0.801	0.760	0.991	0.769
		98	0.232	0.124	0.005	0.246	-	0.199	0.240	0.009	0.231
Me	mc										
n			102	98	99	109	104	99	96	79	93
		100	1.000	1.000	0.995	0.968	1.000	0.949	1.000	1.000	1.000
		98	-	-	0.005	0.032	-	0.051	-	-	-
Pgm-1	mc										
n			80	93	95	99	91	80	89	76	59
		100	0.887	0.935	0.832	0.884	0.923	0.994	0.978	0.980	0.890
		98	0.112	0.065	0.168	0.116	0.077	0.006	0.022	0.020	0.110
Pgm-2	mc										
n			70	69	51	81	87	52	77	62	44
		100	0.850	0.841	0.882	0.926	0.931	0.885	0.864	0.976	0.966
		98	0.150	0.159	0.118	0.074	0.069	0.115	0.136	0.024	0.034
Sdh-2	hp										
n			59	64	33	51	43	38	38	13	28
		100	0.466	0.500	0.485	0.471	0.419	1.000	1.000	0.385	0.536
		98	0.534	0.500	0.515	0.529	0.581	-	-	0.615	0.464
Sdh-3	hp										
n			40	21	8	21	36	38	38	16	13
		100	0.825	1.000	1.000	0.976	0.986	1.000	1.000	1.000	1.000
		98	0.175	-	-	0.024	0.014	-	-	-	-
Xdh-1	hp										
n			94	89	85	88	88	70	75	52	74
		100	0.697	0.831	0.753	0.841	0.795	0.993	0.527	0.731	0.277
		98	0.303	0.169	0.247	0.159	0.205	0.007	0.473	0.269	0.723
Xdh-2	hp										
n			75	60	50	60	66	34	55	53	23
		100	0.520	0.333	0.470	0.175	0.144	0.338	0.373	0.255	0.152
		98	0.480	0.667	0.530	0.825	0.856	0.662	0.627	0.745	0.848

[a] Loci *Ald, αGpd, Gapdh, Gpi, Idh, Mdh-1, Mdh-2, Mpi-1, Mpi-2, Pgd, Pgm-3, Sdh-1* showed no allelic variation in all samples analysed.

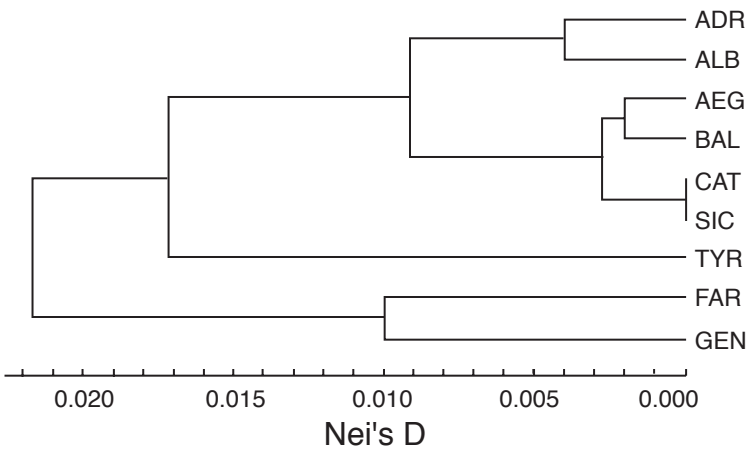

FIG. 2. – UPGMA clustering by Nei's (1978) genetic distances among local populations. Abbreviations for localities are as in Table 1.

TABLE 4. – General genetic variability in analysed samples (standard error in parentheses). Population abbreviations are as in Table 1.

Population	Sample size, mean*	Mean No. of alleles per locus	Percentage of polymorphic loci**	Mean Heterozygosity Direct-count	Expected
ADR	75.5 (5.2)	1.4 (0.1)	43.5	0.135 (0.040)	0.142 (0.040)
AEG	77.8 (6.9)	1.4 (0.1)	39.1	0.085 (0.029)	0.092 (0.032)
ALB	67.9 (8.8)	1.4 (0.1)	43.5	0.103 (0.033)	0.111 (0.036)
BAL	76.3 (7.6)	1.5 (0.1)	47.8	0.082 (0.023)	0.098 (0.030)
CAT	80.1 (6.9)	1.4 (0.1)	39.1	0.068 (0.024)	0.072 (0.027)
FAR	62.8 (6.8)	1.3 (0.1)	30.4	0.047 (0.021)	0.52 (0.025)
GEN	73.5 (6.2)	1.3 (0.1)	34.8	0.073 (0.029)	0.079 (0.033)
SIC	57.3 (7.1)	1.3 (0.1)	34.8	0.055 (0.026)	0.063 (0.030)
TYR	58.7 (8.6)	1.4 (0.1)	39.1	0.090 (0.032)	0.088 (0.032)

*Only polymorphic loci were considered.**0.99 polymorphism criterion

The direct-count mean heterozygosities agreed with those expected under Hardy-Weinberg equilibrium. This was confirmed by chi-square goodness-of-fit of observed genotype frequencies which resulted, with few exceptions, conform to Hardy-Weinberg expectations. Only three tests deviated from expected values, due to marginally significant heterozygote deficiency (population from Adriatic Sea for *Pgm-2* and population from Balearic Islands for *Sdh*-2 and *Ao*).

TABLE 5. – Matrix of Nei's (1978) genetic distance among sampling sites. Population abbreviations are as in Table 1.

	ADR	AEG	ALB	BAL	CAT	FAR	GEN	SIC	TYR
ADR	-								
AEG	0.009	-							
ALB	0.004	0.003	-						
BAL	0.012	0.002	0.008	-					
CAT	0.015	0.002	0.006	0.003	-				
FAR	0.027	0.013	0.021	0.016	0.022	-			
GEN	0.023	0.017	0.021	0.020	0.025	0.010	-		
SIC	0.014	0.002	0.006	0.004	0.000	0.023	0.023	-	
TYR	0.023	0.017	0.020	0.015	0.015	0.037	0.016	0.013	-

TABLE 6. – Summary of Wright's *F*-statistics.

Locus	F_{IS}	F_{IT}	F_{ST}
Ao	0.024	0.191**	0.171**
G6pdh	-0.080*	-0.060	0.019**
Ldh-1	-0.046	-0.039	0.007
Ldh-2	0.020	0.106**	0.088**
Me	-0.043	-0.010	0.032**
Pgm-1	-0.076*	-0.036	0.037**
Pgm-2	0.118**	0.140**	0.025**
Sdh-2	0.090	0.281**	0.210**
Sdh-3	0.241**	0.337**	0.127**
Xdh-1	0.127**	0.290**	0.187**
Xdh-2	0.114*	0.183**	0.078**
Mean	0.067**	0.181**	0.122**

(*) P<0.05, (**) P<0.01

Genetic distances among the Mediterranean populations of *Nephrops norvegicus* were moderate, but relatively high in all pairwise comparisons including Faro, Genoa and Tyrrhenian samples (Table 5). The UPGMA dendrogram failed to reveal a clear geographical pattern of genetic differentiation among investigated populations (Fig. 2). However, a higher affinity is highlighted between Faro and Genoa populations. Some differences of these two samples from the other collection sites is caused by the presence of an unique allele, *Sdh-2*^{100}, in Faro and Genoa populations (Table 3). Specimens from Tyrrhenian Sea are also divergent from all other populations, due to the higher frequency of the allele *Xdh-1*^{98} (Table 3). The six remaining samples clustered together. The cophenetic correlation was 0.871.

A significant mean F_{IT} value, even though few individual loci were significant, showed that there was some structuring within populations (Table 6). Over all loci the mean F_{ST} value was 0.122, this means that 12.2% of the total genetic variation results from differences between populations, with 87.8% coming from within-population variation. Highly significant mean F_{ST} value for the total data set demonstrated significant differentiation among populations. All loci but *Ldh-1* contributed to the significant mean F_{ST} value (Table 6). The average estimate of gene flow calculated by Wright's (1943) method gave a value of $Nm = 1.80$.

DISCUSSION

Our estimates of mean heterozygosity for *Nephrops norvegicus* from Adriatic Sea and Alboran Sea are slightly higher than those reported in previous studies on other decapod species (De Matthaeis *et al*., 1983; Nelson and Hedgecock, 1980; Chow *et al*., 1988; Sardà *et al*., 1995), whereas mean heterozygosities of the other populations are consistent with those of the above mentioned studies. Mantovani and Scali (1992) analysed by allozyme electrophoresis two samples of *N. norvegicus* from the Adriatic Sea and found mean heterozygosity per locus values of 0.033 and 0.036. These values, markedly lower than those reported herein, could be due to the different set of enzymes studied and to the small number of specimens analysed for each population. The extended range of mean heterozygosity values detected in the populations analysed does not exhibit any geographical structuring and probably these values are determined by stochastic variations occurring in single populations.

The analysis of genetic differentiation among populations made by Nei's (1978) genetic distance index showed levels of homogeneity among popula-

tions from Adriatic Sea, Alboran Sea, Balearic Islands, Aegean Sea, Catalan Sea and Sicily Channel; whereas those from Tyrrhenian Sea, Genoa and Faro showed greater levels of differentiation. The UPGMA cluster analysis, based on Nei's (1978) genetic distance matrix, reflected the degree of population structuring and does not depict a clear geographical pattern in the distribution of genetic variation (Fig. 2). Despite the relatively low values of Nei's genetic distance, there are signals of a certain population substructuring as shown by the mean value of F_{ST}, thus Mediterranean Norway lobster populations cannot be necessarily seen as a pure single genetic unit. The analysis of genetic differentiation made by *F*-statistics gave significant mean values of F_{IS}, F_{IT} and F_{ST} gave evidence that allele frequencies varied on range-wide and local scales, among and within populations. In particular, the mean value of standardised variance in allele frequencies (F_{ST} = 0.122) is evidence of a significant degree of species substructuring, according to Workman and Niswander (1970) test. This genetic chaotic distribution is determined by spatially heterogeneous allele frequencies in which local variation may be as high as long-distance variation (Johnson and Black, 1982). The estimated average value of Nm = 1.80 suggests that gene flow among Mediterranean Norway lobster populations is not restricted. In fact, assuming neutrality of genetic markers, as a rule of thumb, a value of Nm>1 is interpreted as evidence of gene flow sufficient to prevent differentiation due to genetic drift (Cabe and Alstad, 1994). Our average estimate of gene flow is consistent with the dispersal capabilities of the species, if we assume that Mediterranean populations of *N. norvegicus* have an average larval life-span of 50 days, similar to that observed in a population from Irish Sea (Hill, 1990). In fact, it is generally admitted that long-life larval planktonic stages favour gene flow resulting in little differentiation among local populations, even over large geographical distances, whereas short or null dispersal periods give significant differences between marine populations (Avise, 1994). However, despite the dispersal strategy adopted by the species, we cannot exclude the presence of mechanisms of local natural selection, favouring different alleles in different demes.

On the basis of the results of the present study, the species appears fragmented in groups, or islands, which replace a fraction of their residents with individuals migrating at random from a large collection of local populations. This last image is partially in agreement with the variability, even if low, of vital parameter estimates as well as reproductive and morphometric features recorded in several sites within the Mediterranean basin. (Gamulin-Brida *et al*., 1972; Froglia and Gramitto, 1979, 1981, 1987; Orsi Relini and Relini, 1989; Biagi *et al*. 1990a, 1990b, 1990c; Mori *et al*., 1993, 1994; Sardà, 1995; 1998). Therefore, among the models of population genetic structure that have been developed to assist managers in predicting the consequences of the exploitation of a biological resource, *N. norvegicus* seems to fit the island model (Wright, 1931), in a background of consistent gene flow. Moreover, there are evidences that local differences could be based on small genetic diversity and not only due to ecological and/or habitat differences (Sardà, 1995). Our allozyme study on *N. norvegicus* indicated that the genetic population structuring of this species in Mediterranean is characterised neither by panmixia nor by isolation by distance, but the chaotic distribution of the intra- and inter-population genetic variability appears arranged according to the island model.

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